

PROCEEDINGS
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PSEUDARCHASTERINAE (ECHINODERMATA,
ASTEROIDEA) OF THE ATLANTIC

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Goniasterid sea stars are an important part of the Atlantic echinoderm fauna. This family contains the subfamily Pseudarchasterinae, which has two genera in the Atlantic, *Pseudarchaster* and *Paragonaster*. These genera have been a great source of difficulty. They have been confused with astropectinid genera by previous workers, and there are a large number of invalid nominal species. The latter is due to several species which display considerable amounts of intra-specific morphological variation and have wide geographic and bathymetric distributions. Thus, the Pseudarchasterinae of the Atlantic are reviewed, with a large number of revisions being made.

This research was supported by National Science Foundation grant GB-4936. The abbreviations used in the material studied sections are as follows: BMNH—British Museum (Natural History); IOM—Institut d'Océanographique de Monaco; MCZ—Museum of Comparative Zoology, Harvard University; MNHN—Museum National d'Histoire Naturelle; UMML—Rosensteil School of Marine and Atmospheric Sciences, University of Miami; USNM—National Museum of Natural History, Smithsonian Institution.

Subfamily Pseudarchasterinae Sladen, 1889 (emended)

Abactinal plates paxilliform. Unpaired (but not recurved) median spine at apex of each mouth plate pair.

The feature that separates this subfamily from the more primitive genera of the Goniasterinae is the unpaired median spine. This is formed by the fusion of the two median spines. Sometimes these do not fuse so that in some specimens one or two of the mouth plate pairs bear a pair of median spines.

Pseudarchaster Sladen, 1885

- Pseudarchaster* Sladen, 1885, p. 617; 1889, p. 109.—Verrill, 1899, pp. 189–190.—Fisher, 1911, pp. 179–180.—Koehler, 1924, p. 180.—Mortensen, 1927, p. 86.—Djakonov, 1950, pp. 43–44.—Bernasconi, 1963, pp. 4–5; 1964, p. 254.
- Aphroditaster* Sladen, 1885, p. 612; 1889, pp. 116–117.—Fisher, 1919, p. 228.
- Astrogonium* (pars) Perrier, 1894, pp. 338–342.—Koehler, 1909, pp. 64–65.
- non *Astrogonium*: Müller and Troschel, 1842, p. 52.

Diagnosis: Several rows of abactinal plates extending far along arm; usually more than one row reaching terminal plate. Unpaired (but not recurved) median spine at apex of each mouth plate pair.

Discussion: Sladen (1889, p. 117) separated *Aphroditaster* from *Pseudarchaster* on the basis of “the longitudinal arrangement of the adambulacral armature and the presence of the remarkable ‘fascioles’ on the post-adambulacral plates.” The remarkable “fascioles” are actually pectinate pedicellariae, which are found in several species of *Pseudarchaster*. The “longitudinal arrangement of the adambulacral armature” does not refer to the furrow spines, which are in an arc, i.e., the furrow margin is curved. The subambulacral spines are fairly regularly arranged, but well within the range of variation in *Pseudarchaster*.

Pseudarchaster and *Aphroditaster* were named in the same paper (Sladen, 1885). Mortensen (1927, p. 86), as first reviser, made *Aphroditaster* the junior synonym of *Pseudarchaster*.

Type-species: *Pseudarchaster discus* (by subsequent designation: Verrill, 1899, p. 189).

A KEY TO THE SPECIES OF *PSEUDARCHASTER* FROM THE ATLANTIC

1. Actinal and inferomarginal plates bearing conical spines three to five times longer than wide *gracilis*
- Actinal and inferomarginal plates bearing flattened lanceolate spines one to three times longer than wide; or spines sometimes absent 2
2. Pectinate pedicellariae along suture of each mouth plate pair *discus**
- No pedicellaria on mouth plate pairs 3
3. Actinal plates usually bearing lanceolate spines *parelii*
- Actinal plates usually lacking lanceolate spines *tessellatus*

* Limited to Antarctic and subantarctic waters.

Pseudarchaster gracilis (Sladen, 1889)

Figures 1–2

- Aphroditaster gracilis* Sladen, 1889, pp. 117–120, pl. 17, figs. 1–2, pl. 18, figs. 7–8.—Verrill, 1899, p. 195.—Fisher, 1919, pp. 227–228.

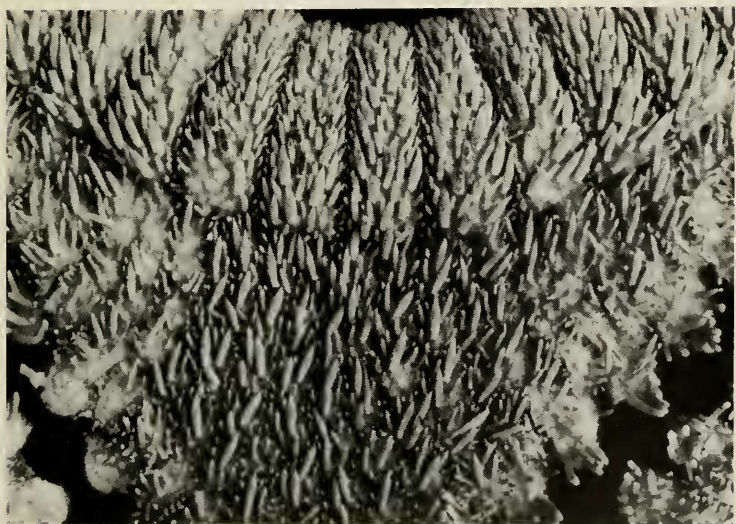
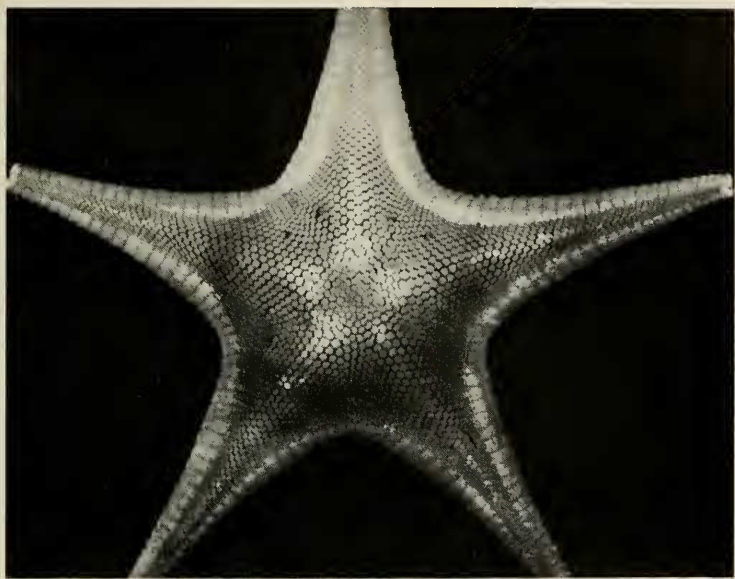


FIG. 1. *Pseudarchaster gracilis* (Sladen), lectotype of *P. concinnus*: top, abactinal view, $0.5\times$.—bottom, actinal view, $2.5\times$.

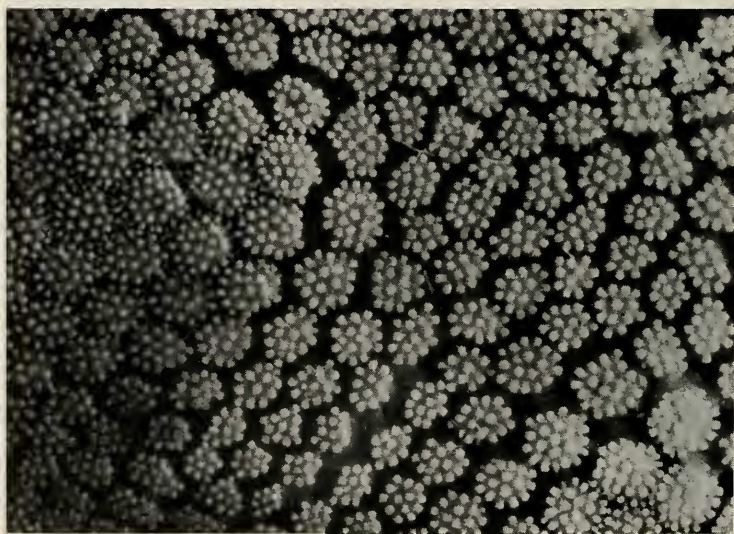
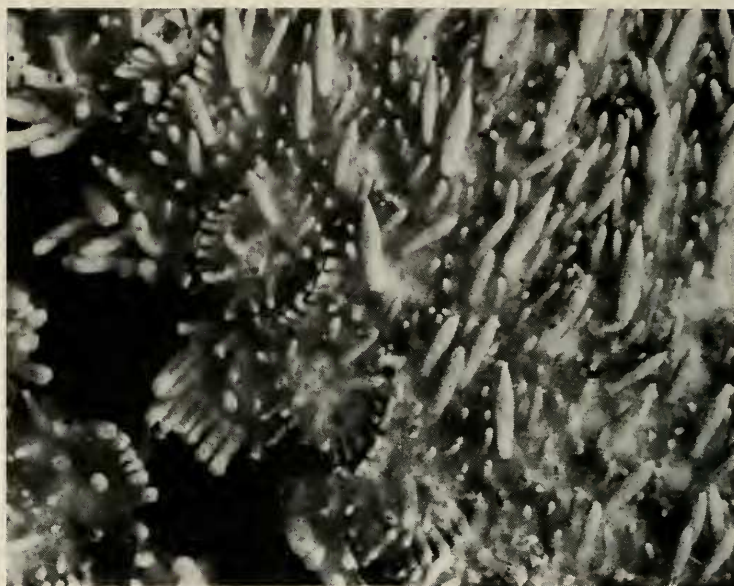


FIG. 2. *Pseudarchaster gracilis* (Sladen), lectotype of *P. concinnus*: top, actinal view, 7 \times .—bottom, abactinal view, 4 \times .

Pseudarchaster concinnus Verrill, 1894, pp. 250–255; 1895, p. 132; 1899, p. 193, pl. 30, figs. 3–3b.—H. L. Clark, 1941, pp. 31–32.—Madsen, 1951, p. 89.—A. H. Clark, 1954, p. 375.

Astrogonium gracile.—Perrier, 1894, pp. 342, 354.

Astrogonium aphrodite Perrier, 1894, pp. 342, 354, pl. 21, fig. 2, pl. 23, fig. 2.

Astrogonium necator Perrier, 1894, pp. 350–352, pl. 23, fig. 1.—Koehler, 1909, pp. 74–75.

Pseudarchaster aphrodite.—Verrill, 1899, p. 195.

Pseudarchaster necator.—Verrill, 1899, p. 195.

Pseudarchaster ordinatus Verrill, 1899, pp. 194–195, pl. 30, figs. 4–4b.—A. H. Clark, 1954, p. 375.

Astrogonium eminens Koehler, 1907, pp. 34–37; 1909, pp. 68–71, pl. 16, figs. 3–6.

Astrogonium aequabile Koehler, 1907, pp. 37–40; 1909, pp. 66–68, pl. 11, figs. 1–4.

Astrogonium marginatum Koehler, 1909, pp. 71–73, pl. 14, figs. 1–4.

Pseudarchaster gracilis.—Mortensen, 1927, p. 86.—Macan, 1938, p. 355.

Material studied: 80 specimens. Holotype: R = 58 mm, r = 14 mm, R/r = 4.1; 37°26'N, 25°13'W, 1830 m, *Challenger* sta. 78, 10 July 1873, BMNH 1890.5.7.106.—41°29'N, 65°36'W, 2174 m, *Albatross* sta. 2706, 27 August 1886, USNM 14944 & E11297, 3 spec., (lectotype and paralectotypes of *Pseudarchaster concinnus* Verrill).—40°17'N, 67°26'W, 1515 m, *Albatross* sta. 2533, 15 July 1885, USNM 33315, 4°C, 1 spec.—39°32'N, 29°02'W, 1900 m, *Princesse-Alice* sta. 1334, 13 August 1902, IOM, (holotype of *Astrogonium aequabile* Koehler).—39°20'N, 26°55'W, 1940 m, *Princesse-Alice* sta. 863, 1 August 1897, IOM, 2 spec., (syntypes of *Astrogonium eminens* Koehler).—39°11'N, 30°45'W, 1846 m, *Princesse-Alice* sta. 698, 18 July 1896, 1 spec., (syntype of *Astrogonium eminens* Koehler).—38°40'N, 26°01'W, 1805 m, *Princesse-Alice* sta. 1331, 9 August 1902, IOM, (holotype of *Astrogonium marginatum* Koehler).—38°38'N, 30°41'W, 1258 m, *Talisman* sta. 127, 1883, MNHN 330, 4°C, 3 spec., (syntypes of *Astrogonium necator* Perrier).—29°03'N, 88°16'W, 592 m, *Albatross* sta. 2376, 11 February 1885, USNM 10345, 8°C, 2 spec.—28°34'N, 86°48'W, 613 m, *Albatross* sta. 2396, 13 March 1885, USNM 18438 (holotype of *Pseudarchaster ordinatus* Verrill).—24°17'N, 82°34'W, 320–437 m, R/V *Gerda* sta. 968, 2 February 1968, 1 spec.—16°53'N, 61°55'W, 750–842 m, M/V *Oregon* sta. 6703, 21 May 1967, 2 spec.—16°35'N, 80°10'W, 576 m, M/V *Oregon* sta. 3560, May 1962, 7°C, 2 spec.—15°39'N, 61°10'W, 650 m, M/V *Oregon* sta. 5929, 5 March 1966, 1 spec.—13°31'N, 81°54'W, 549 m, M/V *Oregon* sta. 1920, 12 September 1957, 1 spec.—13°25'N, 82°01'W, 549 m, M/V *Oregon* sta. 1918, 12 September 1957, 1 spec.—13°22'N, 82°04'W, 549 m, M/V *Oregon* sta. 1929, 13 September 1957, 1 spec.—12°44'N, 82°14'W, 641 m, M/V *Oregon* sta. 1911, 11 September 1957, 1 spec.—12°40'N,

82°18'W, 641 m, M/V *Oregon* sta. 1910, 11 September 1957, 1 spec.—12°33'N, 82°20'W, 641 m, M/V *Oregon* sta. 1908, 11 September 1957, 1 spec.—11°49'N, 69°24'W, 366 m, M/V *Oregon* sta. 4421, 4 October 1963, 1 spec.—11°43'N, 69°10'W, 381 m, *Albatross* sta. 2125, 18 February 1884, USNM 7076, 10.5°C, 1 spec.—11°40'N, 62°27'W, 403 m, M/V *Oregon* sta. 2771, 15 April 1960, 3 spec.—11°35'N, 64°35'W, 1409–1629 m, R/V *Pillsbury* sta. 719, 20 July 1968, 5 spec.—11°35'N, 62°41'W, 388–458 m, M/V *Oregon* sta. 2353, 23 September 1958, 5 spec.—11°33'N, 62°09'W, 586–608 m, R/V *Pillsbury* sta. 478, 2 August 1966, 1 spec.—08°11'N, 56°12'W, 2672–2736 m, R/V *Pillsbury* sta. 681, 14 July 1968, 1 spec.—07°46'N, 54°35'W, 547 m, M/V *Oregon* sta. 10602, 10 May 1969, 1 spec.—07°44'N, 54°19'W, 550 m, M/V *Oregon* sta. 4300, 23 March 1963, 6 spec.—07°37'N, 55°24'W, 1221–1336 m, R/V *Pillsbury* sta. 672, 11 July 1968, 8 spec.—07°34'N, 56°21'W, 1318–1345 m, R/V *Pillsbury* sta. 682, 14 July 1968, 3 spec.—07°30'N, 55°29'W, 805 m, M/V *Oregon* sta. 10624, 17 May 1969, 3 spec.—07°21'N, 53°15'W, 550 m, M/V *Oregon* sta. 4294, 21 March 1963, 10°C, 13 spec.—0.3°50'N, 02°33'W, 1949–1986 m, R/V *Pillsbury* sta. 34, 29 May 1964, 1 spec.

Diagnosis: Bases of paxillae not imbricate. Actinal and inferomarginal plates covered by both small, terete spinules and long, conical spines. One pectinate pedicellaria between every two adjacent actinal plates along row contiguous to adambulacra. Five to 10 adambulacral furrow spines; seven to 11 mouth furrow spines.

Description: Five arms. $R = 109$ mm, $r = 35$ mm, $R/r = 3.1$.

General form stellate with wide, rounded interbranchial arcs.

Abactinal plates paxillose, extending to terminal plates. Paxillae having short pedicels with rounded tops bearing large, rounded, flattened central granules (tabulate in profile) and one peripheral row of short, slender spinelets. Papulae confined to large radial areas. Six papular pores surrounding each plate, each pore containing single papula.

Superomarginal and inferomarginal plates corresponding; 78 plates in each series. Lateral angle of superomarginals compressed so that plates broad and mainly in vertical plane. Superomarginals about four times as wide as long in interbranchial arc; width decreasing distally so that most distal pair less than twice as wide as long. Superomarginals completely covered by large, rounded, flattened granules; granules along lateral margins about half as large as others. Inferomarginals covered by short, terete spinules interspersed among conical spines about five times larger.

Each actinal plate covered by terete spinules and one to four lanceolate spinules. Actinal spines and spinules similar to those on inferomarginals. One pectinate pedicellaria between every two adjacent actinal plates along row contiguous to adambulacra; pedicellaria along entire width of plate.

Adambulacral plates rectangular (wider than long); with angular

furrow margin bearing six to nine cylindrical furrow spines with blunt tips. Subambulacral spines irregularly arranged; similar to actinal spinules but more widely spaced. One to three long, conical spines in center of each adambulacral plate.

Mouth plates moderately prominent; each plate bearing 11 furrow spines similar to adambulacral furrow spines. Large, thick, unpaired median spine at apex of each mouth plate pair. Rest of each plate covered by 12 or 13 spinules along suture and row of two to four spinules between suture and furrow spines. Proximal spinule in each row similar to and slightly smaller than furrow spines; spinules grading into actinal spinules distally.

Madreporite rhombic, small (about one and one-half times size of adjacent abactinals); located about one-third distance from center of disk to middle of interbranchial arc.

Type: British Museum (Natural History) cat. no. 1890.5.7.106.

Type-locality: 37°26'N, 25°13'W, 1830 m, *Challenger* sta. 78.

Distribution: In the western Atlantic this species is known from the northeast coast of the United States, 41°29'N–40°17'N, 1515–2174 m; and throughout the Caribbean, from the northern Gulf of Mexico to Surinam, 320–2736 m. It is known from the Azores in 1095–1940 m. In the eastern Atlantic it occurs off the west coast of Africa, from the Tropic of Cancer to the equator, 1090–1986 m. The known temperature range is 3.5°–10.5°C.

Discussion: The range of R/r is 2.5–3.7; most adult specimens fall between 2.8 and 3.2. The abactinal surface extends to the terminal plates in about 95 percent of the specimens I examined, but several have one to four superomarginals in contact medially. The flattened superomarginal plates of the lectotype of *P. concinnus* are "pushed in," so that they are mainly in the vertical plane. In most specimens the superomarginals are mainly in the horizontal plane. The spines on the actinal and inferomarginal plates are conical and three to five times as long as wide. The actinal surface ranges from very spinose to having scattered spines. Pectinate pedicellariae are always present along the row of actinal plates adjacent to the adambulacrals. There are five to 10 furrow spines and seven to 11 mouth furrow spines.

Most goniasterids release their eggs through the many papular pores but in *Pseudarchaster gracilis* two pores on the edge of each interradius (for each pair of interradiial gonads) are enlarged and the unbranched gonoduct leads only to these pores. The presence of these large gonopores suggests that the species produces large, yolky eggs. This type of egg usually either develops directly or gives rise to short-term, non-feeding larvae.

Remarks: It is necessary to designate a lectotype and paralectotypes for *Pseudarchaster concinnus* Verrill. There are eight extant syntypes in the National Museum of Natural History, Smithsonian Institution, from three stations. Four specimens (*Albatross* sta. 2528) are *Mediaster*

bairdi and one specimen is *Pseudarchaster parelii* (Albatross sta. 2060). The three specimens from Albatross sta. 2706 are *Pseudarchaster gracilis* (as *Pseudarchaster concinnus*) and I designate the largest specimen ($R = 109$ mm, $r = 35$ mm), upon which the original description was based, the lectotype. The two smaller specimens ($R = 73$ mm and $R = 47$ mm) are designated paralectotypes.

Pseudarchaster parelii (Düben and Koren, 1846)

Figure 5

- Astropecten parelii* Düben and Koren, 1846, pp. 247–248, pl. 7, figs. 14–16.—Hoffmann, 1882, pp. 8–9.
- Archaster parelii*.—M. Sars, 1861, pp. 35–38, pl. 3, figs. 1–2.—Norman, 1865, pp. 119–120.—Lütken, 1871, p. 236.—Verrill, 1874, p. 504.—Möbius and Bütschli, 1875, p. 148.—Perrier, 1875, pp. 347–348.—Danielssen and Koren, 1881, p. 268.—Verrill, 1882, p. 140; 1885, p. 543, pl. 13, fig. 37.—Appellöf, 1896, p. 11; 1897, p. 13.
- Archaster parelii* var. *longobranchialis* Danielssen and Koren, 1876, p. 17; 1884, pp. 88–89.
- Astrogonium fallax* Perrier, 1885, pp. 37–38; 1894, pp. 347–350, pl. 23, fig. 4, pl. 25, fig. 4.—Koehler, 1909, p. 71, pl. 18, fig. 2.—Grieg, 1921, p. 21, pl. 5, fig. 1.
- Plutonaster (Tethyaster) parelii*.—Sladen, 1889, p. 102.—Sluiter, 1895, p. 51.
- Pseudarchaster intermedius* Sladen, 1889, pp. 115–116, pl. 19, figs. 3–4, pl. 42, figs. 5–6.—Verrill, 1894, pp. 249–250; 1895, pp. 131–132; 1899, p. 190, pl. 30, figs. 1–1b.
- Plutonaster parelii*.—Bell, 1892, p. 63.—Grieg, 1896, pp. 5, 12; 1897, p. 37.—Ludwig, 1900, pp. 449–450.
- Astrogonium annectens* Perrier, 1894, pp. 343–345, pl. 23, fig. 5, pl. 24, fig. 1.—Koehler, 1895, p. 453.—Perrier, 1896, p. 45.—Koehler, 1909, p. 65.
- Astrogonium hystrix* Perrier, 1894, pp. 345–347, pl. 23, fig. 3, pl. 24, fig. 2.
- Pseudarchaster intermedius* var. *insignis* Verrill, 1895, p. 132.
- Pseudarchaster tessellatus* var. *arcticus* Sluiter, 1895, p. 51.
- Pseudarchaster fallax*.—Verrill, 1899, pp. 190–191, pl. 30, figs. 2–2a.—Koehler, 1921, p. 2.—Macan, 1938, p. 355.
- Pseudarchaster granuliferus* Verrill, 1899, pp. 192–193, pl. 30, figs. 6–6a.—Macan, 1938, p. 355.
- Pseudarchaster annectens*.—Verrill, 1899, p. 195.—Macan, 1938, p. 355.
- Pseudarchaster hystrix*.—Verrill, 1899, p. 195.—Macan, 1938, p. 355.
- Astrogonium longobrachiale* Koehler, 1907, pp. 30–33.
- Astrogonium parelii* var. *longobrachiale*.—Koehler, 1909, pp. 75–83, pl. 14, figs. 8–12, pl. 15, figs. 7–8, 10–12.—Mortensen, 1913, p. 329.
- Tethyaster parelii*.—Süssbach and Breckner, 1911, pp. 202–203.
- Pseudarchaster parelii*.—Fisher (pars), 1911, pp. 202–203.—Farran,

1913, pp. 13–14.—Mortensen, 1924, p. 20.—Koehler, 1924, pp. 180–182, pl. 3, figs. 14–16.—Mortensen, 1927, pp. 87–88, fig. 49.—Macan, 1938, p. 356.—Einarsson, 1948, p. 10.—Djakonov, 1950, pp. 44–45, fig. 184.

Astrogonium parelii.—Grieg, 1912, pp. 5–6.

Material studied: 87 specimens. 72°26'N, 18°00'W, 366 m, BMNH 1969.6.12.136, 4.5°C, 1 spec.—61°10'N, 00°34'E, 132 m, BMNH 1947.-8.15.608, 1 spec.—Shetland Islands, 311 m, BMNH 1900.4.1.381, 1 spec.—Hardangerfjord, coll. Norman, BMNH 98.5.3.1056, 2 spec.—59°13'N, 04°35'E, 213 m, BMNH 1947.8.15.607, 2 spec.—44°01'N, 63°20'W, 202 m, *Speedwell* sta. 108, 20 September 1877, USNM 33289, 2°C, 1 spec.—43°32'N, 59°22'W, 202 m, *Albatross* sta. 2704, 23 August 1886, USNM 14982, 1 spec.—43°03'N, 63°39'W, 156 m, *Challenger* sta. 49, 20 May 1873, BMNH 90.5.7.105, 1.5°C, 4 spec., (syntypes of *Pseudarchaster intermedius* Sladen).—42°49'N, 68°50'W, 95–165 m, *Bache* sta. 21, 16 September 1873, USNM 24558, 6°C, 1 spec.—42°10'N, 66°46'W, 225 m, *Albatross* sta. 2060, 31 August 1883, USNM 21641, 1 spec. (syntype of *Pseudarchaster concinnus* Verrill).—41°47'N, 65°38'W, 1240 m, *Albatross* sta. 2528, 13 July 1885, USNM 11285, 3.5°C, 1 spec.—41°41'N, 65°46'W, 222 m, *Albatross* sta. 2526, 13 July 1885, USNM 12083, 1 spec.—40°10'N, 67°09'W, 2480 m, *Albatross* sta. 2571, 1 September 1885, USNM 11818, 3°C, (holotype of *Pseudarchaster intermedius* var. *insignis* Verrill).—39°57'N, 69°16'W, 838 m, *Fish Hawk* sta. 1029, 14 September 1881, USNM 24560 & 24800, 4.5°C, 3 spec.—39°55'N, 70°28'W, 725 m, *Fish Hawk* sta. 952, 23 August 1881, USNM 9960, 4.5°C, 1 spec.—39°52'N, 70°56'W, 609 m, *Albatross* sta. 2186, 2 August 1884, USNM 8026 & 24561, 4.5°C, 4 spec.—39°49'N, 71°02'W, 667–891 m, *Fish Hawk* sta. 893, 2 October 1880, USNM 9741 & 24559, 4.5°C, 12 spec.—39°23'N, 33°46'W, 1384 m, *Princesse-Alice* sta. 213, 2 August 1888, IOM, 1 spec.—39°17'N, 70°32'W, 896 m, *Albatross* sta. 2214, 22 August 1884, USNM 7945, 4°C, 1 spec.—38°38'N, 73°11'W, 445 m, *Albatross* sta. 2232, 12 September 1884, USNM 8108, 6°C, 2 spec.—38°37'N, 30°41'W, 1258 m, *Talisman* sta. 126, August 1883, MCZ 48, 3.5°C, 2 spec., (syntypes of *Astrogonium fallax* Perrier).—38°35'N, 73°05'W, 1015 m, *Albatross* sta. 2744, 18 September 1886, USNM 16248 & 16303, 4°C, 2 spec.—38°28'N, 73°22'W, 796 m, *Fish Hawk* sta. 1049, 10 October 1881, USNM 4121 & 9742, 4.5°C, 5 spec.—38°20'N, 28°05'W, 1550 m, *Princesse-Alice* sta. 683, 7 July 1896, IOM, 1 spec.—37°59'N, 73°49'W, 813 m, *Albatross* sta. 2171, 20 July 1884, USNM 7659, 4°C, 1 spec.—37°35'N, 31°46'W, 1440 m, *Talisman* sta. 131, 12 August 1883, MNHN 326c, 4 spec., (syntypes of *Astrogonium fallax* Perrier).—32°39'N, 76°51'W, 875 m, *Albatross* sta. 2677, 6 May 1886, USNM 18443, 4°C, 6 spec.—32°28'N, 77°21'W, 645 m, *Albatross* sta. 2626, 21 October 1885, USNM 18446, 3 spec.—32°24'N, 76°56'W, 966 m, *Albatross* sta. 2628, 21

October 1885, USNM 18434, 2 spec.—24°33'N, 84°23'W, 3532 m, *Blake* sta. 31, 1877–78, MNHN 331, 2 spec.—23°21'N, 80°23'W, 869 m, *Atlantis* sta. 2991, 14 March 1938, MCZ 3928, 2 spec.—20°44'N, 18°07'W, 1495 m, *Talisman* sta. 96, 14 July 1883, MNHN 327, 4.5°C, 14 spec.—16°54'N, 63°12'W, 1260 m, *Albatross* sta. 2751, 28 November 1887, USNM 18448, 4.5°C, (holotype of *Pseudarchaster granuliferus* Verrill).

Diagnosis.—Bases of paxillae imbricate. Actinal and inferomarginal spines lanceolate, never more than three times as long as wide. Actinal pectinate pedicellariae variable. Four to seven adambulacral furrow spines; six to eight mouth furrow spines.

Description.—Five arms. $R = 48$ mm, $r = 17$ mm, $R/r = 2.8$.

General form stellate with wide, rounded interbrachial arcs.

Abactinal plates paxillose, extending to terminal plates. Paxillae having short pedicels with rounded tops bearing large, rounded, flattened central granules (tabulate in profile) and one peripheral row of short, slender spinelets. Bases of paxillae six lobed, imbricate. Papulae confined to large radial areas. Six papular pores surrounding each plate, each pore containing single papula.

Superomarginal and inferomarginal plates corresponding; 64 plates in each series. Lateral angle of superomarginals compressed so that plates broad and mainly in vertical plane. Superomarginals three to four times as wide as long in interbrachial arc; width decreasing distally so that most distal pair slightly less than twice as wide as long. Superomarginals completely covered by large, rounded, flattened granules; granules along lateral margins about half as large as others. Inferomarginals covered by squamiform granules; one to six enlarged into flattened, lanceolate spinules one to four times larger.

Each actinal plate covered by squamiform granules similar to those on inferomarginals. Some plates bearing one or two flattened, lanceolate spinules. Proximal actinal plates bearing pectinate pedicellariae formed by marginal granules of adjacent plates.

Adambulacral plates approximately square; with angular furrow margin bearing five to seven cylindrical furrow spines with blunt tips. Subambulacral spines irregularly arranged; first one or two irregular rows about two-thirds as tall as furrow spines; one or two more irregular rows similar to actinal granules.

Mouth plates moderately prominent; each plate bearing six furrow spines similar to adambulacral furrow spines. Large, thick, unpaired median spine at apex of each mouth plate pair. Rest of each plate covered by 10 spinules along suture and row of two to four spinules between suture and furrow spines. Proximal spinule in each row similar to and slightly smaller than furrow spines; spinules grading into actinal spinules distally.

Madreporite rhombic, small (about one and one-half times size of

adjacent abactinals); located about one-third distance from center of disk to middle of interbranchial arc.

Type: Not traced.

Type-locality: Off Kristiansund, Norway, 550 m.

Distribution: In the western Atlantic this species is known from the northeast coast of the United States (44°26'N to Florida) and the West Indies, 100–3000 m. It is known from Greenland (366 m) and the Azores (1250–1400 m). In the eastern Atlantic it is known from off Norway from the Murman coast south to Christiana (72°N–58°N); the Shetland Islands and Ireland. The bathymetric range in the eastern Atlantic is 75–2500 m. The known temperature range is 1.5°–6°C.

Discussion: Because pectinate pedicellariae may be absent, poorly formed or well formed, a discussion of them is pertinent. I have observed live specimens of *Pseudarchaster* which appeared to have no pedicellaria, but in which groups of spines acted as pedicellariae. When the animals were preserved there were no signs of pedicellariae. In some specimens the pedicellariae are well formed and obvious, but in others they are poorly formed.

The enlarged spinules of the actinal and inferomarginal plates range from absent to several on each plate. They are always flattened and lanceolate and never more than three times longer than wide.

The R/r ranges from 2.2 to 3.4. The long and short armed forms are each represented in the major faunal provinces. Specimens with no enlarged spines (the basis for the establishment of *P. granuliferus*) are similarly distributed.

This species, like many other goniasterid species, has a wide geographic and bathymetric range. There is also a wide range of such prominent characters as general form (R/r) and the actinal granulation. I have carefully analyzed a large number of characters for a large number of specimens and could find no basis for separation.

Pseudarchaster tessellatus is very close to *P. parelii* and they may be conspecific. A better knowledge of the Mauritanian region may show continuous distribution along the eastern Atlantic, as in the western Atlantic.

Pseudarchaster parelii differs from *P. gracilis* in having the bases of the paxillae imbricate; often lacking or having poorly developed pedicellariae; having short, flattened, lanceolate spines on the actinal and inferomarginal plates; and having fewer adambulacral and mouth furrow spines.

Pseudarchaster discus, from the Magellanic region, is closely related to *P. parelii* and differs from it by having a pectinate pedicellaria along the suture of each mouth plate pair and having longer, more conical, more numerous spinules on the actinal and inferomarginal plates.

The species from the Pacific that Fisher (1911) considered to be *Pseudarchaster parelii* with the subspecies *P. parelii alascensis*, is a

separate species, *Pseudarchaster alascensis* Fisher. *P. alascensis* differs from *P. parelii* in many small ways, but the major distinction is that it bears spines on the aboral surface of its mouth plates.

Pseudarchaster tessellatus Sladen, 1889

Figures 3-4

Pseudarchaster tessellatus Sladen, 1889, pp. 112-114, pl. 17, figs. 3-4, pl. 18, figs. 9-10.—Verrill, 1899, p. 195.—H. L. Clark, 1923, pp. 253-254; 1926, p. 9.—Mortensen, 1933, pp. 240-241.

Pseudarchaster brachyactis H. L. Clark, 1923, pp. 254-256, pl. 12, figs. 1-2; 1926, pp. 8-9, pl. 2, figs. 1-2.—Madsen, 1950, pp. 211-212, fig. 10.

Material studied: 14 specimens. Syntypes: R = 48 mm, r = 16 mm, R/r = 3.0; R = 32, r = 11, R/r = 2.9; 34°41'N, 18°36'W, 179 m, *Challenger* sta. 141, 17 December 1873, 10°C, BMNH 90.5.7.104.—05°05'N, 04°01'W, 403-586 m, R/V *Pillsbury* sta. 44, 30 May 1964, UMML 40.123, 1 spec.—South West Africa, west of Roast Beef Island, 567 m, *Pickle* sta. 342, 4 May 1921, MCZ 2846, 1 spec.—Cape Colony, west of Saldanha Bay, 168 m, *Pickle* sta. 53, 27 April 1920, MCZ 2848, 2 spec.—Cape Colony, WSW from Saldanha Bay, 561 m, *Pickle* sta. 41, 9 April 1920, MCZ 2847, 2 spec.—off Table Mountain, Cape of Good Hope, 458 m, BMNH 1903.8.1.73-7, 5 spec.—38 miles NE of Cape Point, 576-732 m, *Pieter Faure* sta. 17965, MCZ 2565, 1 spec.

Diagnosis: Bases of paxillae imbricate. Actinals mainly covered by granules; sometimes bearing scattered, incipient, lanceolate spines. Actinal pedicellariae variable. Five to seven adambulacral furrow spines.

Description: Five arms. R = 40 mm, r = 20 mm, R/r = 2.

General form stellate with short, broad, arms. Interbranchial arcs wide, rounded.

Abactinal plates low paxillae; each plate bearing one to six prismatic central granules and eight to fourteen slightly smaller peripheral granules.

Papulae confined to large radial areas. Six papular pores surrounding each plate, each pore bearing single papula.

Superomarginal and inferomarginal plates corresponding; 36 plates in each series. Lateral angle of marginals depressed so that plates very broad and mainly in horizontal plane. Superomarginals about five times as wide as long in interbranchial arc; width decreasing distally so that most distal pair less than two times as wide as long. Superomarginals completely covered by large, rounded, closely crowded granules. No superomarginals in contact medially; abactinal surface extending to terminal plate. Terminal plate small, heart-shaped.

Inferomarginals about four times as wide as long in interbranchial arc, becoming almost square distally. Outer third of inferomarginals covered by rounded granules slightly larger and taller than those on supero-

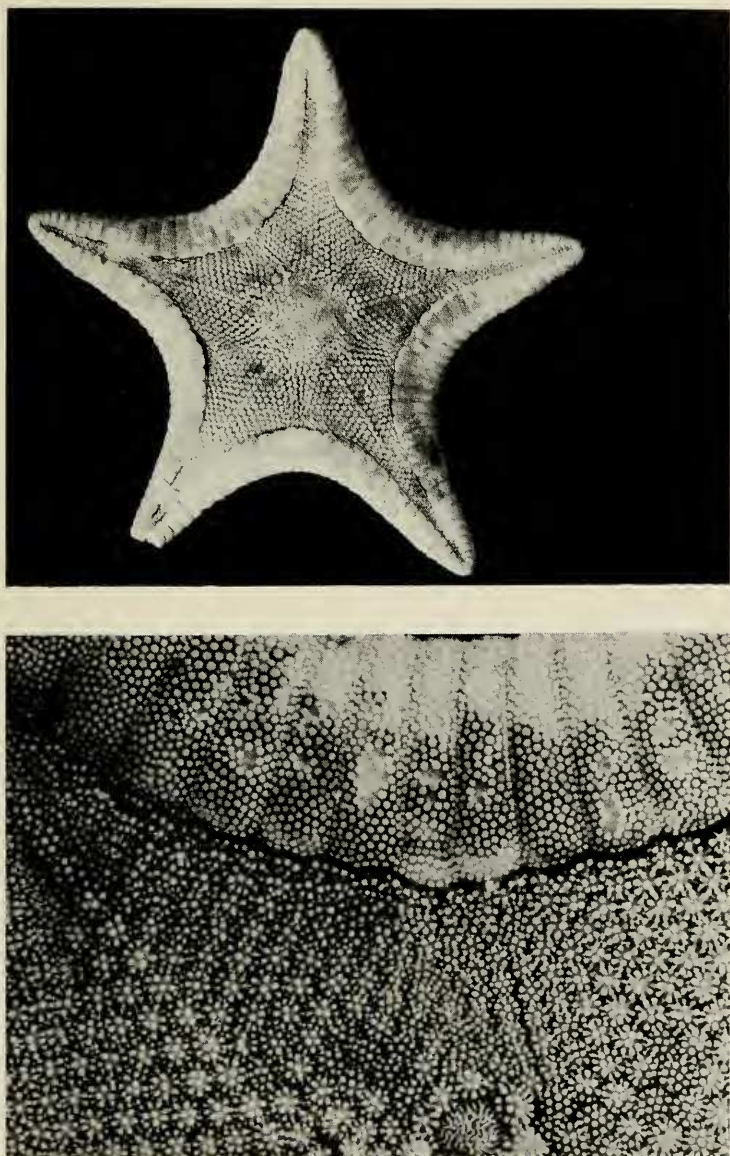


FIG. 3. *Pseudarchaster tessellatus* Sladen, specimen from R/V Pillsbury sta. 44: top, abactinal view, 0.8 \times .—bottom, abactinal view, 5 \times .

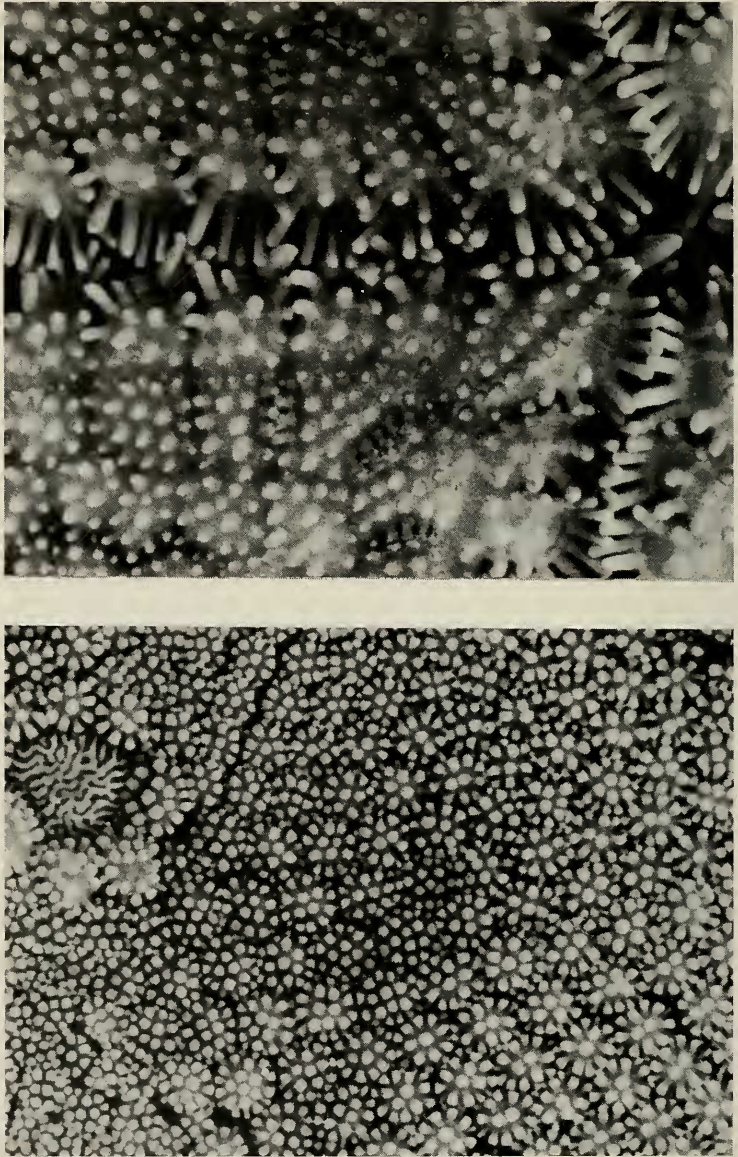


FIG. 4. *Pseudarchaster tessellatus* Sladen, specimen from R/V Pillsbury sta. 44: top, actinal view, 8.5 \times .—bottom, abactinal view, 11 \times .

marginals. Inner two-thirds bearing rounded granules slightly smaller than those of superomarginals; one to six granules enlarged into short, stout, conical spines.

Actinal intermediate area restricted to disk. Actinal plates covered by rounded granules similar to those on inner portion of inferomarginals. Proximal actinal plates bearing pectinate pedicellariae formed by marginal granules of adjacent plates.

Adambulacral plates slightly longer than wide. Angular furrow margin bearing five to seven long, blunt furrow spines; longest spines in center of each series. Subambulacral spines in two to three irregular rows of three to five short, blunt spinules grading into actinal granules.

Mouth plates moderately prominent; each plate bearing seven furrow spines similar to adambulacral furrow spines. Large, thick, unpaired median spine at apex of each mouth plate pair. Rest of each plate covered by row of nine spinules along suture and row of six spinules between suture and furrow spines. Proximal spinule in each row similar to and slightly smaller than furrow spines; spinules grading into actinal granules distally.

Madreporite rhombic, two to three times as large as adjacent abactinals; located one-third distance from center of disk to middle of interbranchial arc.

Type: British Museum (Natural History), cat. no. 90.5.7.104 (2 syntypes).

Type-locality: False Bay, South Africa, 34°41'N, 18°36'W, 179 m, *Challenger* sta. 141.

Distribution: This species is found on the west coast of Africa, from Cape Palmas to Capetown, 168–732 m. The only known temperature record is 10°C.

Discussion: *Pseudarchaster brachyactis* was separated from *P. tessellatus* on the basis of its shorter arms, wider marginal plates and the greater number of abactinal plates along the arms (H. L. Clark, 1923 and 1926). Some of the specimens I examined are intermediates and I consider the characters used for separating the species to be invalid. This case is very similar to the long-armed and short-armed forms found in *Pseudarchaster parelii*. In fact, *Pseudarchaster tessellatus* is very similar to *P. parelii* and may prove to be a junior synonym.

Paragonaster Sladen, 1885

Paragonaster Sladen, 1885, p. 617; 1889, p. 310.—Perrier, 1894, pp. 355–358.—Fisher, 1911, p. 163.

Diagnosis: Single row of large, flat (not paxilliform) abactinal plates along most of arm; always reaching terminal plate. Unpaired (but not recurved) median spine at apex of each mouth plate pair.

Type-species: *Paragonaster ctenipes* (by subsequent designation: Fisher, 1919, p. 228).

A KEY TO THE SPECIES OF *PARAGONASTER* FROM THE ATLANTIC

1. R/r greater than four; actinal plates bearing scattered, small spines *subtilis*
 R/r less than three; actinal plates bearing crowded, large spines *grandis*

Paragonaster subtilis (Perrier, 1881)

Figures 5-6

Goniopecten subtilis Perrier, 1881, p. 26; 1884, pp. 168, 183, 187, 253-254, pl. 5, figs. 3-4; 1885a, p. 41; 1885b, p. 884.—Sladen, 1889, p. 726.

Archaster formosus Verrill, 1884, pp. 383-384; 1885, pp. 519, 543.

Pentagonaster elongatus Perrier, 1885a, p. 38.

Paragonaster cylindratus Sladen, 1889, pp. 311, 314-318, 655, 693, 713, 752, pl. 51, figs. 3, 4, pl. 53, figs. 3, 4.—Perrier, 1894, p. 357.—Verrill, 1894, p. 257; 1899, p. 196.

Paragonaster formosus.—Verrill, 1894, p. 257; 1895, p. 137; 1899, p. 196.

Paragonaster elongatus.—Perrier, 1894, pp. 35, 357, 362-363, pl. 21, fig. 3, pl. 24, fig. 4.—Verrill, 1899, p. 196.

Paragonaster strictus Perrier, 1894, pp. 35, 357, 363-365, pl. 25, fig. 5.—Verrill, 1899, p. 196.

Paragonaster subtilis.—Perrier, 1894, pp. 31, 35, 40, 357, 358-362, pl. 23, fig. 5, pl. 24, fig. 3.—Verrill, 1899, p. 196.—Koehler, 1909, pp. 86-87, pl. 4, fig. 2.—Grieg, 1921, pp. 20-21.—Mortensen, 1927, p. 79.—Macan, 1938, p. 361.—Madsen, 1951, p. 89.

Material studied: 36 specimens. Holotype: R = 60 mm, r = 13 mm, R/r = 4.6; 24°33'N, 84°23'W, 3514 m, *Blake* sta. 31, 1877-78, MCZ 464, 4°C.—39°49'N, 70°32'W, 1058 m, *Albatross* sta. 2215, 22 August 1884, USNM 6621, 4°C, 1 spec.—39°49'N, 68°29'W, 2675 m, *Albatross* sta. 2043, 30 July 1883, USNM 9081, 3.5°C, 4 spec., (syntypes of *Archaster formosus* Verrill).—39°33'N, 68°27'W, 2846 m, *Albatross* sta. 2042, 30 July 1883, USNM 9083 & 14294, 3.5°C, 8 spec., (syntypes of *Archaster formosus* Verrill).—39°23'N, 68°25'W, 2943 m, *Albatross* sta. 2041, 30 July 1883, USNM 9082 & 14295, 3.5°C, 4 spec., (syntypes of *Archaster formosus* Verrill).—39°22'N, 71°24'W, 2543 m, *Albatross* sta. 2564, 11 August 1885, USNM 12045, 3°C, 1 spec.—39°19'N, 71°24'W, 2602 m, *Albatross* sta. 2563, 11 August 1885, USNM 12046, 3°C, 1 spec.—38°59'N, 70°07'W, 2826 m, *Albatross* sta. 2711, 16 September 1886, USNM 15168, 1 spec.—38°38'N, 27°26'W, 2995 m, *Talisman* sta. 131, 22 August 1883, MNHN 332, 3 spec., (syntypes of *Pentagonaster elongatus* Perrier).—38°22'N, 70°18'W, 3341 m, *Albatross* sta. 2714, 17 September 1886, USNM 15171, 1 spec.—38°20'N, 79°09'W, 3402 m, *Albatross* sta. 2713, 17 September 1886, USNM 15174, 1 spec.—

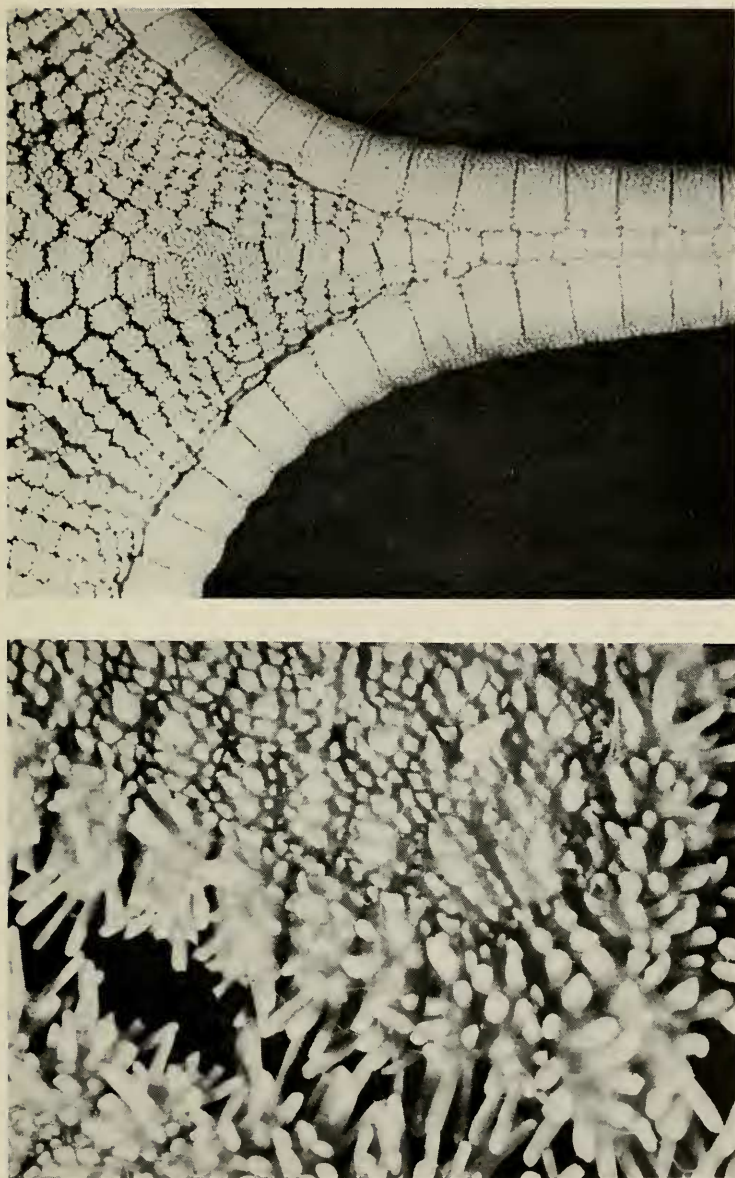


FIG. 5. Top, *Paragonaster subtilis* (Perrier), syntype of *P. formosus*, abactinal view, 3 \times .—bottom, *Pseudarchaster parelii* (Düben & Koren), holotype of *P. intermedius* var. *insignis*, actinal view, 7 \times .

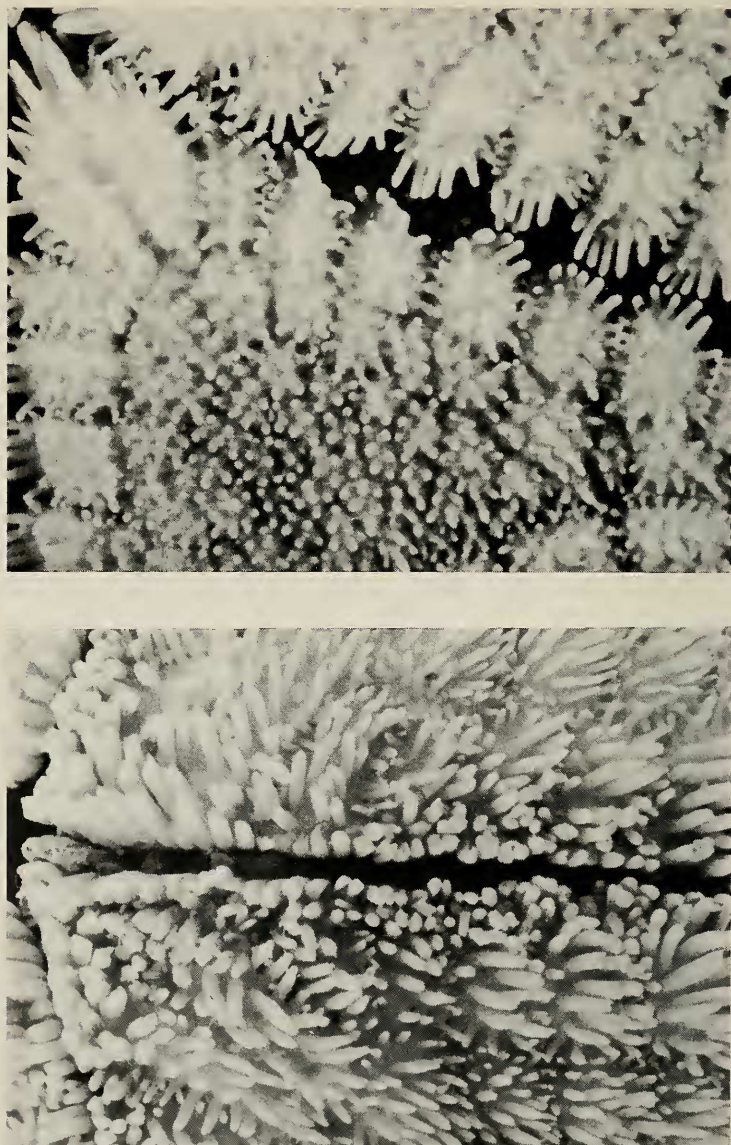


FIG. 6. Top, *Paragonaster subtilis* (Perrier), syntype of *P. formosus*, actinal view, 7 \times .—bottom, *Paragonaster grandis* H. L. Clark, specimen from M/V Oregon sta. 4226, actinal view, 5.5 \times .

38°15'N, 72°03'W, 2917 m, *Albatross* sta. 2174, 21 July 1884, USNM 7963, 1 spec., (syntype of *Archaster formosus* Verrill).—38°09'N, 23°17'W, 4020 m, *Princesse-Alice* sta. 527, 25 June 1895, IOM, 2 spec.—37°17'N, 20°14'W, 4275 m, *Princesse-Alice* sta. 1306, 29 July 1902, IOM, 1 spec.—37°00'N, 71°54'W, 3742 m, *Albatross* sta. 2226, 10 September 1884, USNM 8151, 2.5°C, 2 spec., (syntypes of *Archaster formosus* Verrill).—36°55'N, 22°23'W, 4261 m, *Princesse-Alice* sta. 652, 23 June 1896, IOM, 1 spec.—16°12'N, 24°44'W, 3890 m, *Princesse-Alice* sta. 1150, 25 July 1901, IOM, 1 spec.—25°27'N, 86°06'W, 3103 m, R/V *Alaminos* sta. 68-A-7/4A, 28 July 1968, USNM 279503, 1 spec.—15°48'N, 22°43'W, 3655 m, *Talisman* sta. 102, 19 July 1883, MNHN 333, 3 spec., (syntypes of *Paragonaster strictus* Perrier).—Same as above (*Talisman* sta. 102), MNHN 323b, 1 spec., (labeled *subtilis*).—01°47'N, 24°26'W, 3386 m, *Challenger* sta. 106, 25 August 1873, BMNH 1890.5.7.441, 2.5°C, 2 spec., (syntypes of *Paragonaster cylindricus* Sladen).

Diagnosis: Adults with R/r ratio greater than four. Abactinal plates along arms not wider than long. Inferomarginal and actinal plates not strongly spinose, but at least some actinals bearing spines. Five to eight adambulacral furrow spines.

Description: Five arms. $R = 73$ mm, $r = 17$ mm, $R/r = 4.3$.

General form stellate, with long, narrow arms.

Abactinal surface paxilllose, extending to terminal plates. Paxillae having short pedicels with rounded tops bearing large, rounded flattened central granules (tabulate in profile) and one peripheral row of short, slender spinelets. Single row of large, flat, rectangular abactinals beyond seventh superomarginal, about twice as long as wide. Papulae in large radial areas; lacking in interradial areas, small center of disk and on arms. Six papular pores surrounding each plate, each pore containing single papula.

Superomarginal and inferomarginal plates corresponding; 84 plates in each series. Lateral angle of marginals depressed so that plates broad and mainly in horizontal plane. Superomarginals about three times as wide as long in interbrachial arc; width decreasing distally so that most distal pair less than twice as wide as long. Superomarginals completely covered by large, rounded, flattened granules; granules along lateral margin about half as large as others. Inferomarginal plates covered by spaced, short, terete spinules and six to 10 lanceolate spines, three to four times as large as other spinules.

Actinal plates covered by spaced, terete spinules slightly taller than those on inferomarginals. Most plates covered only by these spinules but some also bearing one or two lanceolate spines slightly taller than those on inferomarginals.

Adambulacral plates large, rectangular (wider than long); with curved furrow margin bearing five to eight cylindrical furrow spines

with blunt tips. Subambulacral spines irregularly arranged; similar to actinal spinules but more widely spaced. One to three lanceolate spines in center of each adambulacral plate.

Mouth plates convex; prominent. Each plate bearing eight to 10 furrow spines similar to those of adambulacrals but slightly larger. Each mouth plate pair bearing single unpaired median spine; median spine about one and one-half times larger than other furrow spines. Rest of mouth plate covered by scattered spinules similar to those on actinals but slightly larger. Spines on oral half along suture enlarged, about one and one-half times larger than others.

Madrepore small, rhombic; located approximately one-half distance from center of disk to middle of interbrachial arc.

Type: Museum of Comparative Zoology, cat. no. 464.

Type-locality: 24°33'N, 84°23'W, 3514 m, *Blake* sta. 31.

Distribution: In the western Atlantic this species occurs along the northeast coast of the United States, 41°07'N–37°00'N, 2455–3742 m, and from the Gulf of Mexico, 3103–3514 m. It is known from the Azores in 2995–4275 m. In the eastern Atlantic it is known from the Bay of Biscay, 4700 m, and the Cape Verde Islands 3386–3890 m. The known temperature range is 1.5°–4°C.

Discussion: There is a strong positive allometric growth of the arms in this species. Eighteen specimens with $r = 5$ –10 mm had R/r ratios of 2.2–3.8 and eight specimens with $r = 11$ –16 mm had R/r ratios of 3.8–4.6. All except two specimens had R/r greater than 3.3. These two specimens measure only $R = 11$ mm, $r = 5$ mm and $R = 15$ mm, $r = 6$ mm.

The spination of the actinal surface varies, but it is never strongly spinose and in adults at least some of the actinal plates bear spines.

Remarks: The many nominal species of *Paragonaster subtilis* have already been synonymized by Grieg (1921), Mortensen (1927), Macan (1938) and Madsen (1951).

This species is not closely related to *P. grandis* and more closely resembles the Indo-Pacific species of this genus.

Paragonaster grandis H. L. Clark, 1941

Figure 6

Paragonaster grandis H. L. Clark, 1941, pp. 32–34, pl. 4, fig. 1.—
A. H. Clark, 1954, p. 375.

Material studied: 3 specimens. Holotype, $R = 80$ mm, $r = 27$ mm, $R/r = 3.0$; 23°10'N, 81°29'W, 311–467 m, *Atlantis* sta. 3000, 21 March 1938, MCZ 3816.—23°06'N, 79°40'W, 540 m, *Atlantis* sta. 3439, 2 May 1939, MCZ 3936, 1 spec. (paratype).—00°18'N, 44°17'W, 275 m, M/V *Oregon* sta. 4226, 9 March 1963, UMML 40.163, 8.5°C, 1 spec.

Diagnosis: R/r less than three. Superomarginals five times as wide

as long in interbrachial arc. Seven to 10 adambulacral furrow spines; subambulacral spines large, crowded.

Description: Five arms. $R = 85$ mm, $r = 35$ mm, $R/r = 2.4$.

General form stellate.

Abactinal surface paxillose, extending to terminal plates. Each paxilla consisting of convex base and short, broad pedicel. Each pedicel bearing large, rounded, flattened central granules and one peripheral row of short, slender spinelets. Single row of large, flat, rectangular abactinals beyond seventh superomarginal; about four times as wide as long proximally, becoming square distally.

Papulae in large radial areas; lacking in large interrational areas, small center of disk and on arms.

Superomarginal and inferomarginal plates corresponding; 58 plates in each series. Lateral angle of marginals depressed so that plates very broad and mainly in horizontal plane. Supermarginals about five times as wide as long in interbrachial arc; width decreasing distally so that most distal pair less than twice as wide as long. Supermarginals completely covered by large, rounded, flattened granules; granules along lateral margin very small, chisel-shaped. Inferomarginals completely covered by closely crowded lanceolate spines; lateral margins bearing small spinelets.

Actinal plates bearing peripheral row of slender spinelets and central group of lanceolate spines similar to those on inferomarginals.

Adambulacral plates large, rectangular (wider than long); with slightly curved furrow margin bearing eight to 10 cylindrical furrow spines with blunt tips. Subambulacral spines irregularly arranged; similar to actinal spines but slightly larger.

Each mouth plate bearing nine to 10 furrow spines similar to those of adambulacrals but slightly larger. Each mouth plate pair bearing single unpaired median spine; median spine slightly larger than other furrow spines. Rest of mouth plate covered by closely crowded spinules similar to subambulacral spinules of adambulacral plates.

Madreporite very small, rhombic; located approximately one-third distance from center of disk to middle of interbrachial arc.

Type: Museum of Comparative Zoology, cat. no. 3816.

Type-locality: 23°10'N, 81°29'W, 311–467 m, *Atlantis* sta. 3000.

Distribution: This species is known from the northern coast of Cuba and from off Brazil, near the equator. The bathymetric range is 275–540 m. The only temperature record is 8.5°C.

Remarks: This species is very distinctive and differs from all the other known species of *Paragonaster* by its small R/r ratio, spinose actinal surface, and large number of adambulacral furrow spines.

H. L. Clark (1941, p. 34) states, "This fine sea-star resembles *Pseudarchaster concinnus* so much not merely in general form and proportions but in the paxillae and the armature of the marginal,

actinal and even the adambulacral plates that it was at first supposed to be simply a peculiar adult stage of the species" The armature of the inferomarginal, actinal and adambulacral plates of *Paragonaster grandis* is very different from that of *Pseudarchaster concinnus*.

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